Title: An alternative explanation for global trends in thermal tolerance

Short title: Explaining thermal tolerance trends

Authors: Nicholas L. Payne[1,2] & James A. Smith[3]

Affiliations: [1]National Institute of Polar Research, 10-3, Midori-cho, Tachikawa, Tokyo 190-8518, Japan 190-8518. [2]University of Roehampton, Holybourne Avenue, London, UK SW15 4JD. [3]University of New South Wales, High Street, Kensington, New South Wales, Australia 2043

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Correspondence: Nicholas L Payne,
University of Roehampton
Holybourne Avenue, London, UK SW15 4JD
Email: nick.payne@roehampton.ac.uk
Ph: +353 83 831 3454

Abstract

Ectotherms from higher latitudes can generally perform over broader temperature ranges than tropical ectotherms. This pattern is thought to reflect trends in temperature variability: tropical ectotherms evolve to be 'thermal specialists' because their environment is thermally stable. However, the tropics are also hotter, and most physiological rates increase exponentially with temperature. Using a dataset spanning diverse ectotherms, we show that the temperature ranges ectotherms tolerate (the difference between lower and upper critical temperatures, and between optimum and upper critical temperatures) generally represents the same range of equivalent biological rates (e.g. metabolism) for cool and warm adapted species, and regardless of latitude or elevation. This suggests geographical trends in temperature variability may not be the ultimate mechanism underlying latitudinal and elevational trends in thermal tolerance. Rather, we propose that tropical ectotherms can perform over a narrower range of temperatures than species from higher latitudes because the tropics are hotter.

Introduction: The temperature-dependence of organism performance (e.g. growth rate, maximum running or swimming speed, or the scope for aerobic metabolism) is often described by a thermal performance curve, where performance rises from a lower critical temperature (T_{crit}) to an optimum (T_{opt}), and subsequently declines to an upper T_{crit}. The temperature range between lower and upper T_{crit} is the thermal tolerance breadth (TTB), and it is a cornerstone of macroecology that TTB increases with latitude and elevation. Since the influential work of Janzen (1967), the global trends in TTB (e.g. Addo-Bediako *et al.* 2000; Sunday *et al.* 2011) are almost universally explained as adaptive responses of organism physiology to the greater temperature variability at higher latitudes and elevations (the 'temperature variability hypothesis'). That is, animals that regularly experience a wide range of temperatures ought to evolve physiologies that tolerate a wide range of temperatures.

When reported in degrees Kelvin or Celsius, temperature measures the average kinetic energy of a substance. Because temperature is directly proportional to average kinetic energy, a given change in temperature at either low (e.g. 5 to 10°C) or high (e.g. 30 to 35°C) temperatures corresponds to the same change in kinetic energy. In contrast, almost all biological rates (e.g. metabolism and biochemical reactive rates) increase exponentially with temperature, according to

$$R_0 e^{-E/kT} \quad (1)$$

where E is activation energy, k is Boltzmann's constant, T is absolute temperature in Kelvin, and R_0 is an organism- and state-dependent scaling coefficient (Brown *et al.* 2004; Dell *et al.* 2011). This is because as temperature increases, an increasingly larger proportion of particles exceed the minimum E required to take part in a reaction. The temperature-dependence of whole-animal performance (thermal performance curves) is governed by the effect of temperature on these lower-level processes (e.g. cellular metabolism and reactive rates) that increase exponentially with temperature; at least over the normal range of activity (0-40°C for most organisms; Brown *et al.* 2004). For example, the temperature-dependence of whole-animal performance in fishes is often measured in terms of the scope for aerobic metabolism, which is the difference between resting and maximum aerobic metabolic rate (Fig. 1). Because the biological rate processes that determine the shape of performance curves proceed more rapidly at higher temperatures, it could be expected that performance will decline more-rapidly on either side of T_{opt} for higher values of T_{opt} (Fig. 1). This effect would result in smaller differences between T_{opt} and T_{crit} for warm-adapted species, and therefore a narrowing of TTB with increasing T_{opt}. Thermal performance curves would also tend to be left-skewed, and they invariably are (Martin & Huey 2008; Angilletta 2009).

If biological rate processes that increase exponentially with temperature largely determine the slopes of the rise and fall in performance on either side of T_{opt} (e.g. Fig. 1), then plotting

thermal performance curves on empirical temperature scales (e.g. in degrees Celsius or Kelvin) should tend to generate narrower TTBs for warm-adapted species than for cool-adapted ones (Fig. 2a), even if the difference in equivalent biological rates at lower and upper T_{crit} (e.g. the resting metabolic rate at upper T_{crit} minus that at lower T_{crit}) is the same (Fig. 2b). Because minimum, mean and maximum temperatures generally increase with decreasing latitude and elevation, it is therefore possible that the difference in kinetic energy (i.e. temperature in degrees Celsius or Kelvin) between lower and upper T_{crit} decreases toward the equator and sea-level because the equivalent difference in biological rates (which underpins thermal performance curves) does not (Fig. 2b). Whether cool and warm adapted species generally maintain the same temperature-dependence of physiological processes (the 'metabolic cold adaptation' hypothesis) is a controversial topic (Holeton 1974; Clarke & Johnston 1999; Addo-Bediako *et al.* 2002; White *et al.* 2012), so whether tropical, temperate and polar ectotherms maintain a similar range of biological rates (e.g. resting metabolism) between lower and upper T_{crit} is uncertain. While the temperature variability hypothesis is almost universally accepted as the explanation for many geographical trends in thermal tolerance, the potential role of temperature *per se* – and its exponential relationship with biological rate processes – is largely unexplored.

In this study, we analysed several datasets on T_{opt} and T_{crit} of diverse ectotherms to explore whether the commonly-observed global trends in thermal tolerance (e.g. Addo-Bediako *et al.* 2000; Sunday *et al.* 2011) could be explained by temperature's exponential influence on biological rate processes rather than by adaptation of ectotherm physiology to temperature variability. We first examined data from fishes and terrestrial lizards to test whether the difference between T_{opt} and T_{crit} varies in a way that is consistent with our prediction about temperature's exponential influence on biological rate processes. Our specific hypothesis was that the difference between T_{opt} and T_{crit} in degrees Celsius would be smaller for warm-adapted species than for cool-adapted ones, but will be the same for warm- and cool-adapted species

when T_{opt} and T_{crit} are expressed as equivalent biological rates *via* the Boltzmann-Arrhenius relationship (equation 1). Next, we analysed an updated, comprehensive global dataset on lower and upper T_{crit} of terrestrial and aquatic ectotherms (Sunday *et al.* 2011) to examine latitudinal and elevational trends in TTB when T_{crit} is expressed as equivalent biological rates instead of in degrees Celsius. In doing so, our general aim was to explore whether global trends in ectotherm thermal tolerance could ultimately be caused by the temperature-dependence of biological rates rather than by adaptation of species to global trends in environmental temperature variability. We tested our hypotheses with data from studies that measured acute, short-term tolerance limits, which do not necessarily represent long-term survival limits of species (Peck *et al.* 2009; Peck *et al.* 2014) because the realised thermal niche of a species is generally narrower than temperatures bounded by lower and upper T_{crit} (Sunday *et al.* 2012; Peck *et al.* 2014). As such, we seek to provide an alternative explanation of trends reported for acute, laboratory-derived thermal tolerance measurements rather than global trends in the temperature ranges that species tolerate over extended periods in the wild.

Materials & Methods:

Two recent comparative papers (Huey *et al.* 2009; Payne *et al.* 2016) reported optimal and critical temperatures in fishes and lizards, and found that T_{opt} is strongly correlated with upper T_{crit} for both groups. However, lower T_{crit} could not be estimated with any degree of certainty for the fish dataset (Payne *et al.* 2016), and T_{opt} was not correlated with lower T_{crit} for terrestrial lizards (Huey *et al.* 2009). Given this, we only explored the relationship between T_{opt} and the upper T_{crit} (the difference between T_{opt} and T_{crit} we call the 'heating tolerance') for those data, and did not examine cooling tolerance. For the fish dataset, upper T_{crit} was estimated by fitting a two-part performance curve to aerobic scope data and extrapolating to zero scope above T_{opt} (see Payne *et al.* 2016 for data inclusion protocols, procedure for fitting of performance curves, and

95% confidence intervals for T_{opt} and T_{crit} estimates), and for lizards, upper T_{crit} was identified as the point where animals lost the righting response (Huey *et al.* 2009). For data on TTB**,** we reanalysed upper and lower T_{crit} of the diverse ectotherms presented in Sunday et al (Sunday *et al.* 2011), and updated this dataset by conducting a literature search of ectotherm critical temperatures published since 2011. Like Sunday *et al.*, we excluded data from our TTB analyses that were derived from latitudes above 60°, because their lower T_{crit} estimates are potentially confounded by the freezing point of water.

We converted each value of T_{opt} and T_{crit} to an equivalent biological rate, *r*, *via* the Boltzmann-Arrhenius relationship (equation 1). Activation energies, *E*, and scaling coefficients, R_0, are known to vary across taxa, so we used different values of *E* and R_0 to convert temperatures to *r* for different animal groups. Gillooly *et al.* (2001) derived separate relationships between temperature and mass-normalised resting metabolic rates (in W g^{-1}) for multicellular invertebrates, fish, amphibians and reptiles, so we adopted their relevant values of *E* (0.788, 0.433, 0.496 and 0.757, respectively) and R_0 ($e^{23.53}$, $e^{10.38}$, $e^{12.59}$ and $e^{22.76}$, respectively) for those four major animal divisions to transform our empirical temperature data (note: we divided all *r* values from the Gillooly paper by 60 to correctly report units of W g^{-1}).

Phylogenetically-informed least squares regression was used to test relationships between T_{opt} and heating tolerance for fish and lizards both in degrees Celsius and *r*. Although the need to account for phylogeny in comparative analyses has been questioned (e.g. Westoby *et al.* 1995), methods that incorporate phylogenetic information into analyses of data derived from multiple species are often considered necessary to account for data non-independence (i.e. closely related species tend to resemble each other; Felsenstein 1985). We were interested in the relationship between T_{opt} and heating tolerance because, under our hypothesis, performance should decline more rapidly above T_{opt} for higher values of T_{opt}, so considered this the most direct test of our hypothesis. We chose not to compare heating tolerance to environmental temperature variability

148 (i.e. the competing traditional hypothesis), because the range of temperatures experienced by a
149 species will vary not only by latitude and elevation, but also by microhabitat, season, through
150 ontogeny, and will be heavily influenced by thermoregulatory behaviour. Given these
151 complexities, we considered such an approach prone to error due to the uncertainty in measuring
152 temperature variation for each species. We built phylogenetic trees for lizards using the PDDIST
153 output published as online material in Huey *et al*. (Huey *et al.* 2009), and for fishes using
154 Betancur-R *et al*. (Betancur-R *et al.* 2013) (trees are presented in S1). Using the arbitrary branch
155 length method of Pagel (Pagel 1992), we conducted phylogenetically independent contrasts using
156 the PDAP package with the software Mesquite (Maddison & Maddison 2011), treating the five
157 sockeye salmon populations as polytomies. Because r was computed using different values of E
158 and R_0 for different animal groups, we did not use phylogenetically informed statistics for the
159 TTB data, and instead used linear models and generalised additive models (GAMs) to examine
160 relationships between latitude and TTB in degrees Celsius and r. GAMs using penalized thin
161 plate regression splines were only fitted to biological rate-equivalent TTBs if AICs were
162 improved over a linear model. GAMs used a basis dimension $k = 6$ to avoid unrealistic smoothers,
163 and were fitted using the 'mgcv' package in R (R Core Team 2015). Like Sunday *et al.* and
164 others (e.g. Addo-Bediako *et al.* 2000), we compared TTB to elevation-corrected latitudes. To
165 further examine the influence of elevation on TTB, we ran additional linear models on the
166 terrestrial ectotherm data for which both latitude and elevation were reported. For these models,
167 we used the uncorrected latitudes from Sunday, and included the interaction term between
168 latitude and elevation to test whether TTB variation across latitude varied by elevation.
169
170 **Results**
171 As reported in the earlier papers (Huey *et al.* 2009; Payne *et al.* 2016), heating tolerance
172 decreases as T_{opt} increases, and this happens at a similar rate for both fishes and lizards (for fishes

[n = 14]: slope = -0.24, intercept = 10.93, phylogenetically-informed least squares t = -2.19, R^2 = 0.29, $P < 0.05$; for lizards [n = 70]: slope = -0.27, intercept = 17.12, phylogenetically-informed least squares t = -5.93, R^2 = 0.34, $P < 0.001$; Fig. 3a). However, when temperatures are expressed as equivalent biological rates, heating tolerance does not vary for different values of T_{opt} for either fishes or lizards (phylogenetically-informed least squares for fishes: t = -0.23, R^2 = 0.004, P = 0.82; for lizards: t = -1.38, R^2 = 0.03, P = 0.17; Fig. 3b). Results were qualitatively the same for fishes when analyses were rerun to exclude those data where extrapolated estimates of CT_{max} were relatively uncertain (i.e. when we excluded the five fish datasets from Payne *et al*. 2016 where 95% CIs for CT_{max} encompassed ≥ 3°C range; for degrees Celsius: n = 9: slope = -0.20, intercept = 9.13, phylogenetically-informed least squares t = -2.68, R^2 = 0.51, $P < 0.05$; for equivalent biological rates: t = -0.51, R^2 = 0.04, P = 0.63) Thus, the difference between T_{opt} and upper T_{crit} in r does not vary between cool and warm adapted (i.e. for different T_{opt}) fishes or lizards.

Our search of recent literature returned TTB measurements from an additional 54 species and this updated dataset of TTBs across latitude for terrestrial and aquatic ectotherms is shown in Fig. 4a and 4b, respectively. For empirical temperature, TTB increases linearly with latitude and with comparable slope and intercept estimates for terrestrial (n = 241; slope = 0.292, intercept = 25.77, t = 11.62, $P < 0.001$) and aquatic (n = 115, slope = 0.183, intercept = 28.66, t = 5.81, $P < 0.001$) ectotherms. In contrast, TTB in terms of equivalent biological rates does not vary with latitude for terrestrial ectotherms (Fig. 4c; GAM edf = 2.48, P = 0.09; LM slope = -7.09×10^{-6}, intercept = 0.005, t = -0.57, P = 0.57) and for aquatic ectotherms, biological rate-equivalent TTB is highest from the equator to ~ 40-50° of latitude, and subsequently declines (Fig. 4d; GAM edf = 2.66, $P < 0.001$; LM slope = -2.18×10^{-5}, intercept = 0.003, t = -6.53, $P < 0.001$). For aquatic ectotherms, rate-equivalent TTB does not decline with latitude when points above 50° latitude are excluded (GAM edf = 2.21, P = 0.07; LM slope = -4.18×10^{-6}, intercept = 0.003, t = -1.02, P = 0.31). For

198 the reduced dataset that included elevation information, empirical TTB generally increased with
199 latitude and elevation, and the effect of elevation on empirical TTB was greater at lower latitudes
200 (significant negative interaction term, n = 148, t = -6.172, P < 0.001; Table S1), but neither
201 latitude, elevation nor their interaction significantly influenced TTB in terms of equivalent
202 biological rates (Table S1). Thus, the average range of equivalent biological rates between lower
203 and upper T_{crit} is maintained across latitude and elevation for terrestrial animals, and across low
204 to mid latitudes for aquatic ectotherms, and declines thereafter. Latitudinal TTB results are
205 qualitatively the same if temperatures for all species are transformed with a single mean R_0 and E,
206 rather than using different R_0 and E for the different major animal divisions.
207
208 **Discussion:**
209 These results support our hypothesis that the higher heating tolerance of cool adapted species
210 arises from maintenance of the same range of equivalent biological rates between T_{opt} and upper
211 T_{crit} among cool and warm adapted species. Similarly, terrestrial ectotherms across all latitudes
212 and elevations maintain the same average range of equivalent biological rates between lower and
213 upper T_{crit} (Fig. 4c; Table S1). In contrast to the case for terrestrial ectotherms, aquatic
214 ectotherms actually exhibit higher rate-equivalent TTBs near the equator than the poles. However,
215 lower T_{crit} of aquatic ectotherms are potentially influenced by the freezing point of water, with
216 tolerance measurements taken on marine ectotherms either limited to temperatures greater than ~
217 - 2.0°C, or conducted on animals frozen in ice (as were most of the higher latitude aquatic data in
218 Fig. 4). An inability to move and extract oxygen from their habitat would undoubtedly confer
219 less plasticity of lower T_{crit} near freezing temperatures for aquatic ectotherms, and indeed, the
220 downward inflection of biological rate-equivalent TTB for aquatic ectotherms occurs at the same
221 latitudes at which lower T_{crit} of those species approaches the freezing point of seawater (~40-60°;
222 Fig. 4d, S2). In other words, the poleward decline in biological rate-equivalent TTB from mid-

latitudes for aquatic ectotherms may be an artefact of their habitat freezing at low temperatures. In general, aquatic ectotherms also tolerate a smaller range of equivalent biological rates than terrestrial ectotherms (both for heating tolerances and TTBs; Fig. 3b, Fig. 4 c-d), and this is unsurprising given oxygen is far less available and more costly to acquire in water than in air (Pörtner 2001; Verberk *et al.* 2011). That is, the demand for oxygen increases with temperature in a similar way for terrestrial and aquatic ectotherms (i.e. via the Boltzmann-Arrhenius relationship), but the challenge of supplying these demands is far greater for aquatic animals. Differential oxygen availability is thought to explain why warming-induced reductions in body size are stronger for aquatic animals than for terrestrial ones (Verberk *et al.* 2011; Forster *et al.* 2012), and could also explain why aquatic animals tolerate smaller changes in their temperature-equivalent biological rates.

Notwithstanding complexities associated with lower T_{crit} of aquatic ectotherms, heating tolerance and TTB data generally support our alternative hypothesis for explaining latitudinal and elevational trends in ectotherm thermal tolerance. However, support for our hypothesis does not necessarily imply rejection of the traditional temperature variability hypothesis, because both hypotheses predict lower empirical TTBs toward lower latitudes and elevations. One way of discriminating between these two potential explanations is provided by heating tolerance data from polar marine ectotherms, because while average temperatures are vastly different between equatorial and polar oceans, temperature fluctuations are similarly small (~ 2°C annual range). Under the temperature variability hypothesis, heating tolerance should be highest for species adapted to intermediate temperatures (i.e. mid-latitudes) and smallest for those adapted to low (i.e. polar) and high (i.e. equatorial) temperatures (conceptualised by the dashed black line in Fig. 5). Conversely, if heating tolerance represents a fixed difference in equivalent biological rates regardless of temperature (as indicated by Fig. 3b), then the relationship between T_{opt} and heating tolerance (Fig. 3a) would actually be curved rather than linear; this theoretical curve is fitted to

fish aerobic scope data in Fig. 5 and extrapolated to lower temperatures (blue circles and solid blue line; see S3 for derivation of the curve and model fitting). Estimates of T_{opt} and upper T_{crit} for aerobic scope in polar fishes are currently unavailable, so we cannot test whether heating tolerance for aerobic scope *per se* in such animals is low (as would be expected under the temperature variability hypothesis; dashed black line in Fig. 5) or high (as would be expected under our biological rate hypothesis; solid blue line in Fig. 5). However, there are data from several polar fishes where T_{crit} was defined differently to our fish dataset (upper T_{crit} data presented in Bilyk & DeVries 2011). Assuming T_{opt} of polar fishes occurs somewhere within the range of environmental temperatures that they normally experience in their natural habitat (mean habitat temperatures are often lower than T_{opt}, but most similar to T_{opt} for ectotherms from thermally stable habitats such as polar oceans; Martin & Huey 2008), and that T_{crit} for aerobic scope approximates other T_{crit} measures (Pörtner & Knust 2007; Pörtner 2010), then the heating tolerance of polar fishes can be estimated; these are shown in Fig. 5 (black data). Calculated in this way, the heating tolerance of those 11 fish species from thermally stable Antarctic waters match extrapolations from the temperate and tropical fish data under our hypothesis remarkably well (the blue curve in Fig. 5 is fitted to, and extrapolated from, blue fish aerobic scope data, not fitted to black polar data). While reliant on some assumptions about T_{opt} and T_{crit} of polar fishes (e.g. whether T_{opt} for aerobic scope lies within the range of temperatures naturally encountered by polar fishes is uncertain; some lower-latitude species have T_{opt} very close to modal habitat temperatures (Eliason *et al.* 2011), whereas others have T_{opt} near the higher temperatures encountered within their range (e.g. Clark *et al.* 2011; Rummer *et al.* 2014)), this comparison is strong evidence that temperature's exponential influence on biological rates (i.e. our new hypothesis) rather than temperature variability (i.e. the traditional explanation) determines the heating tolerance of marine ectotherms, because polar and tropical fishes encounter similarly-small environmental temperature fluctuations, but exhibit vastly different heating tolerance (i.e. ~

15°C versus ~ 3°C, respectively; Fig. 5). Consideration of temperature's exponential influence on biological rates therefore seems to explain the apparent contradiction (Wilson *et al.* 2001; Seebacher *et al.* 2005) that polar marine fishes can tolerate acute exposure to temperatures far exceeding those they would ever experience in nature (sometimes by more than 15°C; Fig. 5; Peck *et al.* 2009), whereas tropical fishes live close to their upper thermal limits (Rummer *et al.* 2014). Still, heating tolerances presented in Fig. 5 were calculated differently for polar and other species, so a more definitive conclusion would come from examining fish aerobic scope data spanning the equator to the poles (should such data become available), and by accounting for the potentially (e.g. Clarke & Johnston 1999 versus White *et al*. 2012) elevated temperature-standardised metabolic rates of polar fishes (the metabolic cold adaptation hypothesis). Interestingly, many polar invertebrates exhibit upper T_{crit} values similar to those of polar fishes (e.g. Peck *et al.* 2009), so exploring how temperature's influence on biological rates affects heating tolerances of non-fish polar ectotherms could prove fruitful.

Importantly, the relatively high heating tolerance of polar fishes does not necessarily imply that these species ought to withstand significant long-term warming beyond current temperatures, because acutely-measured upper T_{crit} is often far higher than temperatures an ectotherm can tolerate for prolonged periods (Peck *et al.* 2009; Peck *et al.* 2014). For example, comparative analyses of Antarctic marine ectotherms indicates survival to temperatures of ~ 8-18°C under experimental warming of 1°C per day, but only 1-6°C under acclimations of several months (Peck *et al.* 2009; Richard *et al.* 2012); similar responses to experimental warming rates have been documented for temperate and tropical ectotherms (Nguyen *et al.* 2011; Morley *et al.* 2016).

There appears to be significant variation in the range of equivalent biological rates ectotherms tolerate at any given latitude or T_{opt} (residuals in Fig. 3b and 4c are large, particularly for terrestrial ectotherms), and it could prove fruitful to explore the relative importance of environmental heterogeneity (similar taxa from the same latitude can display very different

thermal tolerance limits depending on microhabitat differences; e.g. Kaspari *et al.* 2015) and methodological differences in driving this variation. For example, critical and lethal temperature limits are defined and measured in myriad ways, and are strongly influenced by experimental protocols such as warming rates (Nguyen *et al.* 2011), acclimation, and response measures (critical limits are variously defined as the onset of loss of the righting response: Huey *et al.* 2009; lack of response to tactile stimuli: Peck *et al.* 2009; or aerobic metabolic scope: Payne *et al.* 2016; limits that would often be defined as lethal limits given sufficient monitoring durations because life at temperatures that preclude movement, or where resting metabolism cannot be met aerobically, will be necessarily short), and these differences undoubtedly contribute to variation in the equivalent biological rates characterising different species' TTBs (Fig. 4c) and heating tolerances (Fig. 3b). It is also important to note the compelling experimental evidence that ectotherms can adjust their thermal tolerance limits in response to environmental variability (Schaefer & Ryan 2006), and such plasticity might also contribute to the large differences in equivalent rates ectotherms can tolerate at any given latitude or T_{opt}. Nevertheless, the dominant geographical trends in environmental temperature variability do not translate into latitudinal or elevational trends in the range of equivalent biological rates species can tolerate.

Improving our understanding of how temperature regulates thermal tolerance is increasingly important given the rapidly changing climate and mounting evidence that species distributions are closely linked to thermal tolerance limits (Sunday *et al.* 2012; Sunday *et al.* 2014; Payne *et al.* 2016). That temperature variability drives thermal tolerance is a paradigm commonly invoked to explain a range of macroecological patterns such as latitudinal and elevational trends in species range size (Rapoport's rule; Stevens 1989; Chan *et al.* 2016), and to predict that tropical species will be most vulnerable to global warming (Ghalambor *et al.* 2006; Tewksbury *et al.* 2008). Although the temperature variability hypothesis for explaining global trends in thermal tolerance is intuitive, it does not satisfactorily explain several major patterns, such as the very different

heating tolerances between equatorial and polar oceans; both of which are thermally stable habitats. Our consideration of equivalent biological rates suggests the ultimate cause of some of the major global trends lie there instead. Maintenance of equivalent ranges of biological rates across TTBs and heating tolerance also raises interesting questions about thermal specialisation, as an increase in maximum performance for warmer-adapted species ("hotter is better") is often seen to be traded-off for reduced performance breadth, with the total area under the curve kept relatively constant (Levins 1968; Gilchrist 1995). While we generally measure and report temperature in terms of kinetic energy (degrees C or K), few biological or ecological processes are directly proportional to kinetic energy, so it may be insightful (Buckley & Huey 2016; Payne *et al.* 2016) to also investigate temperature-dependent processes on more biologically-relevant scales such as in terms of equivalent biological rates.

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Figure legends:

Figure 1. **Temperature's influence on thermal tolerance breadth: an example for fishes**. In fishes, thermal performance curves (blue lines) are often quantified as the temperature-dependence of 'aerobic scope' – the difference between resting (red line) and maximum (dashed lines) metabolic rates. Like most other biological rates, resting metabolic rate increases exponentially with temperature, so a given value of maximum performance (i.e. the aerobic scope at T_{opt}) will tend to decline more rapidly on either side of T_{opt} for species that have higher

T_{opt} (i.e. warm-adapted species). The difference between lower and upper T_{crit} (the thermal tolerance breadth) will therefore be larger for cool-adapted species than for warm-adapted ones.

Figure 2. **Empirical versus "biological" temperature scales**. Because most biological rates, *r*, increase exponentially with temperature, the larger range of temperatures over which a cool-adapted species can perform (A) may correspond to the same range of equivalent *r* for both cool- and warm-adapted species (B). In this figure, empirical temperatures on the x-axis in A have been converted to equivalent biological rates *via* the Boltzmann-Arrhenius relationship (equation 1 in main text). In reality, species with higher T_{opt} may have higher maximum performance at T_{opt} (the "hotter is better" hypothesis; Kingsolver & Huey 2008; Angilletta *et al.* 2010), and the position of performance curves for a species can shift due to acclimation or relative to T_{crit}, depending on how T_{crit} is defined. While simplified, this figure serves to illustrate the concept of transforming empirical temperatures to equivalent biological rates.

Figure 3. Empirical versus biological rate-equivalent heating tolerance. Heating tolerance of terrestrial lizards (n = 70; green data) and fishes (n = 14; blue data), when T_{opt} and T_{crit} are presented in degrees Celsius (A) and as equivalent biological rates, *r* (B). Both slopes are significant ($P < 0.05$) in A; *NS* indicates neither is significant in B.

Figure 4. Latitudinal trends in ectotherm thermal tolerance breadth, TTB. In both A and B, TTBs (green and blue for terrestrial [n = 241] and aquatic [n = 115] ectotherms, respectively) are presented in degrees Celsius. In both C and D, temperatures have been converted to equivalent biological rates *via* the Boltzmann-Arrhenius relationship (equation 1 in main text). All curves are significant for A, B, and D ($P < 0.001$), whereas neither a linear regression nor GAM was significant for TTB data in C (P = 0.57 and 0.09, respectively).

Figure 5. Heating tolerance of polar fishes. Aerobic scope data for fishes from a range of latitudes (from Fig. 3A; n = 14) are represented by blue circles, and a non-linear model was fitted to these data (blue line; see S3 for derivation of the curve) and extrapolated to lower values of T_{opt}, assuming heating tolerance represents the same average range of equivalent biological rates for any value of T_{opt}. The black dashed line represents a conceptualisation of the temperature variability hypothesis as it relates to marine ectotherms. The estimated (see Discussion) heating tolerances of 11 species of polar fishes are overlaid (black diamonds), i.e. the blue curve was not fitted to the black data from polar fishes. Error bars represent the full range of environmental temperatures experienced in each polar species' environment; ranges used to represent the uncertainty in estimates of T_{opt} and therefore heating tolerance.

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